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ANTLER CYCLES AND BREEDING SEASONALITY OF THE CHITAL (*AXIS AXIS* ERXLEBEN) IN SOUTHERN INDIA[1]

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(*With six text-figures*)

Key words: Antler development, fawning, circannual rhythms, age-specific reproduction, tropical dry evergreen forest, axis deer, *Axis axis*.

Annual cycles of antler renewal and casting, and births in a free-ranging, high-density population of chital or axis deer were studied for 2.5 years in Guindy National Park in southern India. In all the three age-classes (yearling, juvenile, and adult males), seasonality was pronounced and birth seasonality was evident. Occurrence of most births (49%) between December and March, at the onset of the dry season, probably enabled the energetically expensive late-lactation period of females to coincide with the first flush in food availability after the rains. Only adult males attained peak hard antler during the months when most conceptions occurred; the monthly percentage in hard antler. was significantly correlated with fawning 8-9 months later. Time-lag correlations and patterns of antler development showed that the peak in hard antler of juvenile and yearling males occurred 2.5 and 5 months later than in the adult males. Such staggered rutting cycles may reduce inter-male conflict and increase the chances of subordinate age-classes achieving copulation.

Introduction

Breeding cycles of deer are known to be closely linked to annual environmental rhythms in the temperate regions. In the tropics, where environmental rhythms are relatively diffuse and unpredictable, breeding is often considered to be markedly less seasonal or aseasonal (Lincoln 1992 a,b). There is evidence, however, that many mammal species in the tropics and equatorial regions also show distinct seasonality which is influenced by factors such as photoperiod, rainfall, food availability, and genetics (Bronson 1989).

Deer offer a unique opportunity to study breeding seasonality due to their habit of sporting antlers. These bony outgrowths of the cranial frontal bones occur in 36 of the 40 extant deer species, and are grown and cast at roughly annual intervals in consonance with seasonal sexual cycles (Goss 1983, Lincoln 1985, 1992b). In all species that possess antlers, excluding the reindeer (*Rangifer tarandus*), only males carry antlers (Lincoln 1992b). Yearling males in most species produce their first set of antlers on reaching puberty, and successive sets of antlers in ensuing years increase in size and complexity parallel to the increase in body size. Rutting males can be distinguished easily by the exposed, bony, hard antlers they carry, in addition to characteristic sexual behaviour (deVos *et al.* 1967, Goss 1983, Lincoln 1992b, Mishra and Wemmer 1987, Schaller 1967). In addition to antler size and body condition, the reproductive success of males in polygynous species also changes according to the age of the individual

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(Clutton-Brock 1982, 1987). Prime-aged adult males can be expected to rut during the annual peak in female oestrus. If male-male competition for females is high, younger or subordinate males may then be forced to rut at different times of the year when adults are in velvet or exhausted after their rutting activities (Dunbar *et al.* 1990, Hirotani 1994). Monitoring monthly changes in the proportion of males of different age classes in hard antler, along with fawning peaks, can be used to examine breeding seasonality and age-related reproductive strategies of deer.

The chital or axis deer, *Axis axis* Erxleben, is an endemic cervid of south Asia occurring between *c.* 8°N and 30°N in India, Sri Lanka, Nepal, and Bangladesh (Schaller 1967). This, coupled with the fact that it is common and widespread within its range, makes it a suitable representative for research on the ecology of tropical cervids, which have been poorly studied as compared to temperate zone cervids (Lincoln 1985, 1992a,b, Loudon and Brinklow 1992). There have been several studies on the natural history and ecology of chital in India and Sri Lanka where it is native (Barrette 1985, 1987, Berwick 1974, Eisenberg and Lockhart 1972, Johnsingh 1983, Krishnan 1972, Mishra 1982, Mishra and Wemmer 1987, Miura 1981, Schaller 1967, Sharatchandra and Gadgil 1975, Tak and Lamba 1984), and in other countries where it was introduced (Ables 1977, Graf and Nichols 1966). Quantitative information on antler cycles and breeding seasonality is, however, available in only a few studies (Fuchs 1977, Graf and Nichols 1966, Johnsingh 1983, Mishra and Wemmer 1987, Schaller 1967, Sharatchandra and Gadgil 1975). Among these, Fuchs (1977) also examined antler cycles within different age classes of males for a single year.

Reports from studies of captive herds of seasonal synchrony in annual antler and birth cycles have been conflicting (Bubenik *et al.* 1992, Loudon and Curlewis 1988). In the wild, however, studies have generally documented some seasonality (Johnsingh 1983, Mishra and Wemmer 1987, Schaller 1967, Sharatchandra and Gadgil 1975). The pulse of seasonality is seen to be weak, at least some males being in hard antler throughout the year (Fuchs 1977, Mishra and Wemmer 1987, Schaller 1967). It is not clear, however, whether the males rutting outside the peak rut are adults or younger males whose rut is staggered relative to adults — an important aspect of age-related reproductive strategies. This paper presents a comparative account of antler development in different age classes of males, and birth seasonality over 2.5 years in a free-ranging, high density population of chital in southern India. The existence of age-related differences in antler cycles of males is examined in relation to female breeding seasonality and births and compared with those from previous studies on chital and other cervids.

Study Area

Guindy National Park (GNP) is a 2.7 km² park located in the southwest corner of Chennai (Madras) city (13°N, 80°E) in south India. The vegetation, appearing as patches of scrub jungle, thickets, and wooded areas, corresponds to the Tropical Dry Evergreen Forest of Champion and Seth (1968), reclassified as the *Albizia amara* Boiv. community (Puri *et al.* 1989). A detailed description of the park is available elsewhere (Raman *et al.* 1996). The mean annual rainfall is 1215 mm, most of which falls during the northeast monsoon in October-November, though the park receives rain during the pre-monsoon (April-May) and the southwest monsoon (June-September) as well (Fig. 1). The park is home to a small native population of about 50 blackbuck (*Antilope cervicapra* L.) and a high-density population of about 550 chital (212.3 chital/km² during 1991-92, line transect estimate in Raman *et al.* 1996).

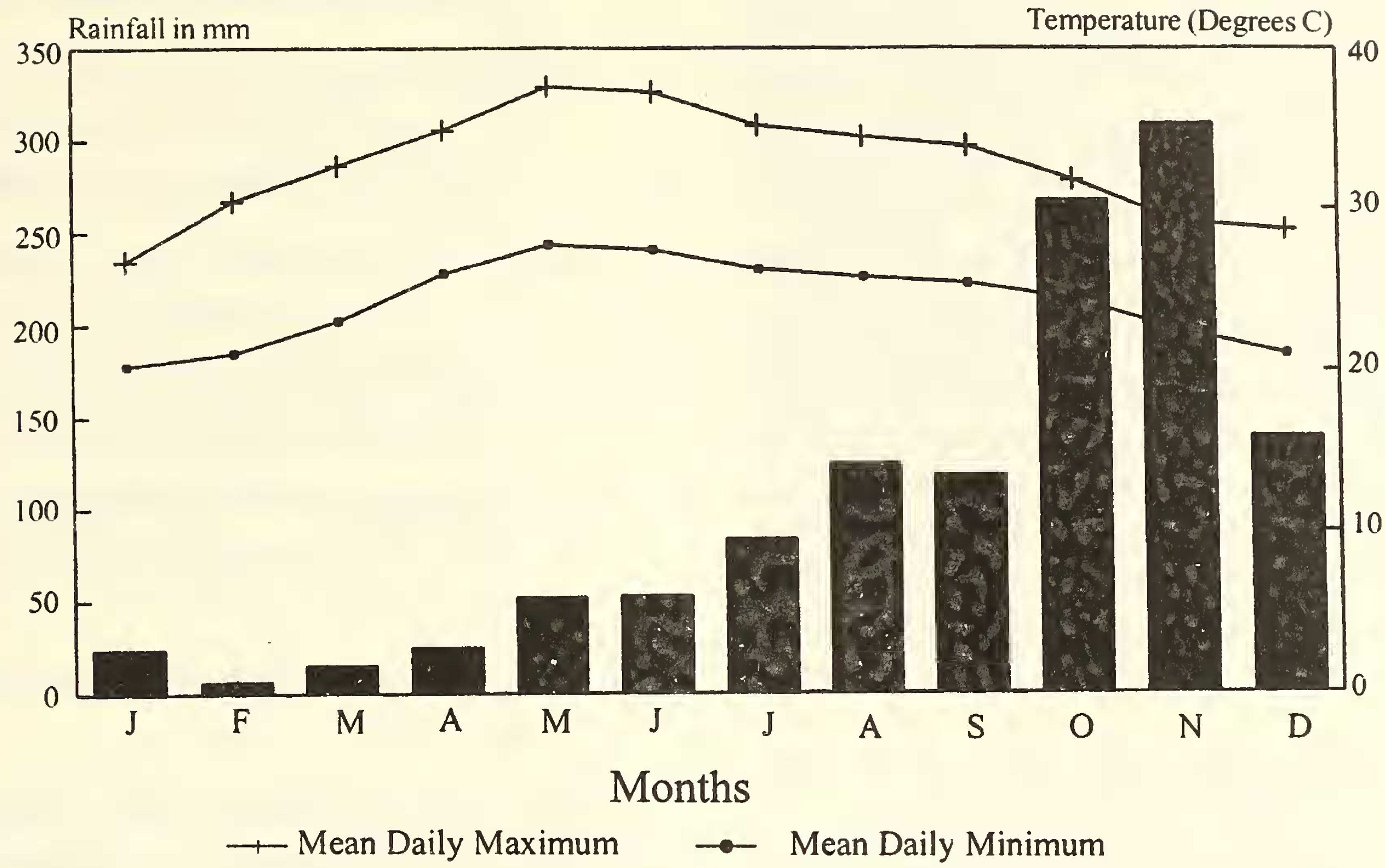

Fig. 1: Rainfall (vertical bars) mean monthly maximum and minimum temperatures for GNP. Data averages for 1931-1960 from the Climatological Table for Chennai (Minambakkam). Rainfall and temperature regimes were similar during the study period 1991-93. (see Raman *et al.* 1996).

Methods

Six months (July-December 1990) of preliminary observations were made on over 500 free-ranging individuals in GNP, concurrent to observations of captive chital in the adjacent Children's Park zoo. Based on these observations, the age-sex and antler-stage classification of chital by Schaller (1967) was substantially refined (see below). A total of 12,866 individual chital were classified into different age-sex and antler categories between January 1991 and May 1993 (sampling with replacement). An average of 444 (range 121-920) chital were classified each month, which comprised, on an average, of 232 adult females (76-488), 35 yearling females (2-67), 35 fawns (2-80), 82 adult males (29-170), 31 juvenile males (6-73), and 32 yearling males (2-74). Around eight field visits were made each month, with 3-5 trips each in the morning (0600 to 1000 h) and evening (1600 to 1900 h), the times of day when animals were most active. Observations were made along established transects, forest trails, and roads using a pair of 7 x 50 binoculars. Accurate classification of individuals was possible because the chital in GNP are generally not very shy of humans and can be approached easily to within 30-50 m, often to less than 20 m. Animals more than 100 m away, and those not seen clearly, were not classified. Bellows (rutting call given by adult males usually consisting of 3-5 loud notes) heard in the field were also recorded.

Age-sex and antler classification

Females could be classified only as adult or yearling females in the field (Schaller 1967). Fawns were classified as small fawns (<2 months) and big fawns (>2 months), based on their height in relation to that of adult females whom they almost invariably accompanied. Fawns could not be sexed in the field. Males were classified into 16 categories (see below) representing different stages of maturity and antler condition within three age groups — yearlings, juveniles and adults. Having these broad groups facilitated distinguishing the age class of individual males irrespective of antler condition, by looking at antler pedicel height (which declines with age), pedicel width, and head and body sizes (which increase with age). The detailed classification of antler development stages within each age class allows the monitoring of seasonal changes at a finer level and identifying the rutting period clearly.

(A) Yearling Males or Spikers, age 10 months - 2 yr) were classified as follows:
- (i) Button Male: Only a stub-like developing pedicel (*c.* 2 cm), completely covered by hair, is visible on the head.
- (ii) Velvet: A blunt, spike-like growing antler covered in fawn-coloured 'velvet' and mounted on a tall (*c.* 4-5 cm) pedicel.
- (iii) Dry Velvet: A pointed spike-like antler, 10-12 cm long, with a thin grey covering of velvet.
- (iv) Hard Spiker: Hard bony antler with no trace of velvet. This includes an intermediate stage, namely, yearlings with the velvet peeling off before the hard antler stage. Such individuals are rarely seen, presumably because this process occurs in just a few days.

(B) Juvenile Males (age 2-3 yr) were classified as follows:
- (i) Cast Yearling: Only the tall pedicel of the yearling is present, with signs of the wound at the burr where the antler was cast.
- (ii) Growing Velvet: Bulbous-tipped antler usually with a small brow tine.
- (iii) Mature Velvet: Antler reaches nearly full length of 20-30 cm and has a rounded (*not* bulbous) tip and a fawn colour.
- (iv) Dry Velvet: Antler is mature, pointed, and covered by a thin but entire covering of dark, greyish velvet.
- (v) Peeling: Strips of velvet usually hang loose from the antler and portions of the bone are visible underneath.
- (vi) Hard: Hard bony antler with no trace of velvet left.

(C) Adult Males (age > 3 yr) — Six adult male classes were considered:

Cast Adult, Growing Velvet, Mature Velvet, Dry Velvet, Peeling, and Hard antler adults were distinguished as in the case of Juvenile Males. Antler beam, pedicel, and body size were larger than for Juvenile Males and enabled unambiguous classification in the vast majority of cases.

Analyses

The percentage of males within each age class in the different stages of antler condition was computed for each month between March 1991 and May 1993. Initially (January-March 1991), adult and juvenile males were not distinguished, hence the data were not included in the age-specific analyses.

For each month, the number of small fawns (age < 2 months) was expressed per 100 adult females to examine seasonality in births. The number of bellows heard during 0600-0900 h and 1600-1900 h was divided by the number of hours spent in the field in those time blocks to get an index of bellowing rate (bellows/hour).

Sinusoidal curves were chosen to fit the data on the annual antler cycles (Batschelet 1981).

The curves were of the form:

$$y = A \cos \frac{\pi}{6} (t - t_{max}) + \bar{H}$$

where: y — percentage of males (of a given age class) in hard antler.

t — month number (ranging from January = 1 to December = 12).

A — amplitude (a measure of the extent or magnitude of the seasonality pulse).

t_{max} — the month which is the peak in the annual cycle,

$\bar{H}$ — annual mean of the monthly percentage of males (of that age class) in hard antler (a constant estimated from the data).

The parameters of the curve have biological relevance (Batschelet 1981: 159). The parameter t_{max} estimates the month (Jan. = 1 to Dec. = 12) when the peak in antler cycles is reached. Similarly, the estimated value of the peak percentage of males in hard antler during the annual cycle is given by $A + \bar{H}$ (when $t = t_{max}$, $y = A \cos (0) + \bar{H} = A + \bar{H}$). Initial estimates of A and t_{max} were derived iteratively and these were used to perform non-linear regression using SPSS/PC + software (Norušis 1990).

TABLE 1

BREEDING SEASONALITY OF ALL CHITAL MALES CONSIDERED TOGETHER AND AS SEPARATE AGE CLASSES*

Male Age Class	Amplitude (A)	Peak month (t_{max})	Mean monthly % in hard antler ($\bar{H}$)	R^2 %	N
All Ages	18.56	7.10	55.4	84.9	26
Yearling	18.35	11.35	45.3	39.7	26
Juvenile	34.24	8.67	60.4	79.6	26
Adult	28.31	6.25	56.9	89.0	26

*Parameter estimates from non-linear sinusoidal curve fitting data in Figure 2. For explanation of parameters see text (Analyses).

To examine temporal differences between antler cycles of different age classes of males, time-lag correlations were used as explained below. This was also used to correlate male peaks in hard antler with births 8-9 months later (this corresponds to the gestation period in chital: English 1992, Rao 1984; see Discussion). In these analyses, a lag of one unit corresponded to one month, and a range of 0-12 lag units was employed. Pearson's product-moment correlation coefficients were computed in each case. The lag at which the maximum significant positive correlation existed between the antler cycles of two age classes of males represented the number of months separating their peaks in hard antler. Similarly, a significant positive correlation between the percentage of males of a given age class in hard antler in a given month and the number of small fawns observed 8-9 months later indicated whether the peaks in hard antler coincided with incidents of mating and conception.

RESULTS

Age-specific antler cycles

Males in hard antlers were seen throughout the year, with 50% (40%) or more males being in hard antler during 8 (10) out of the 12 months of the year (Fig. 2a). When considered by age-class, however, more distinctly seasonal patterns are evident (Fig. 2b-d). The amplitude or extent of the seasonality pulse of all males combined in the analysis was lower ($A = 18.56$), compared to the seasonality of adult or juvenile males coming into hard antler ($A = 28.31$ and 34.24, respectively, Table 1). The extent of seasonality appeared to be low for yearling males ($A = 18.35$), but the curve fit was poor in this case ($R^2 = 0.40$) and the data also suggests a more distinct seasonality than for all males considered together (Fig. 2b *vs* 2a).

A majority (73-91%) of the adult males came into rut and hard antler between March

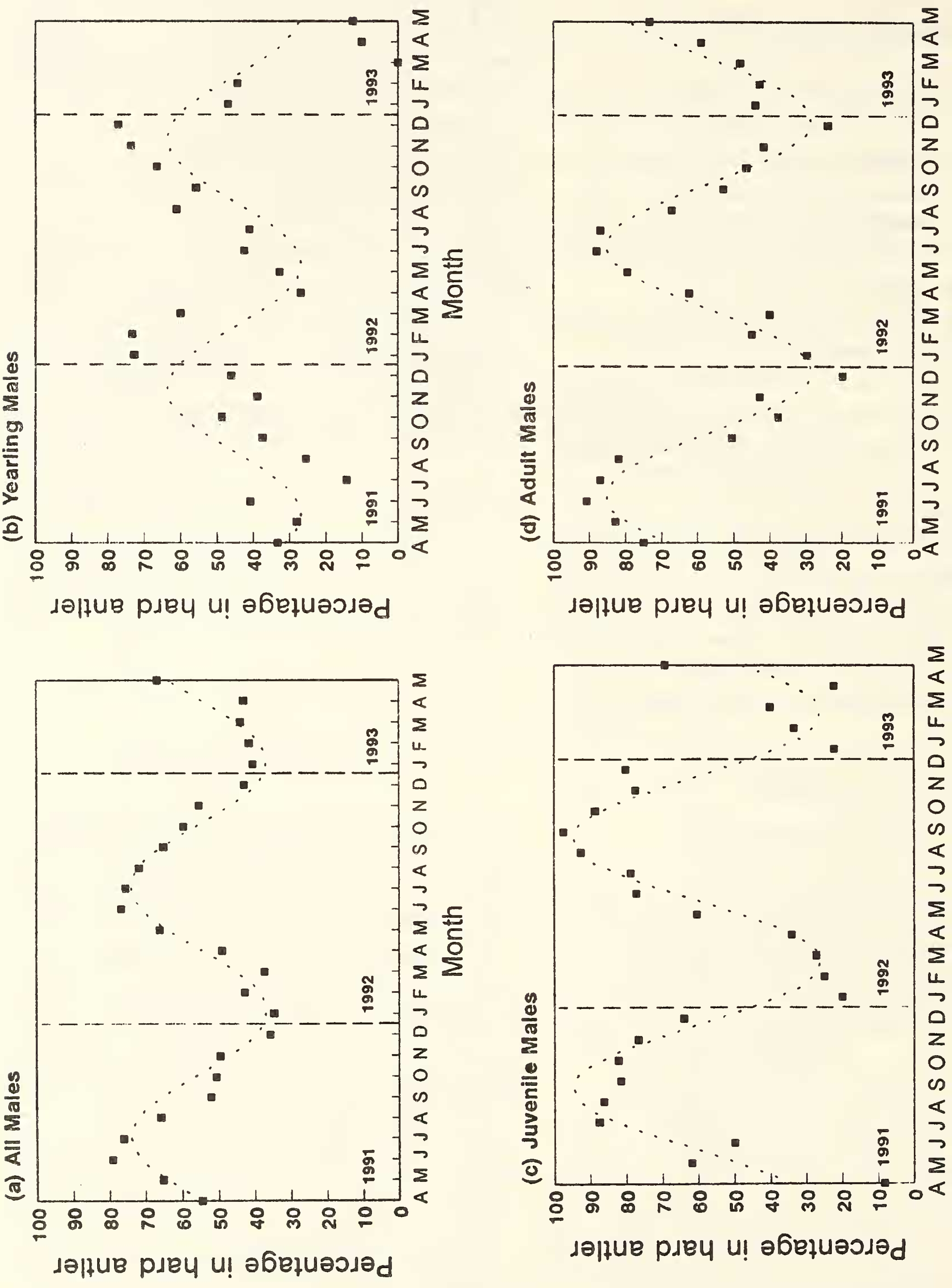

Fig. 2: Seasonality of antler cycles modelled as sinusoidal curves as monthly percentage of (a) All Males, (b) Yearling Males, (c) Juvenile Males, and (d) Adult Males, in hard antler.

and July, with the peak in hard antler being in July (t_{max} = 6.3, Fig. 2d). Most of their rutting activity appeared concentrated between April and July, the period when the number of bellows per hour was highest. Thus, available data for April-December 1991 showed that the percentage of adult males in hard antler during a given month was positively correlated with the number of bellows per hour that month (r = 0.85, df = 7, 2-tailed P = 0.004).

Juvenile males, in contrast to adult males, came into hard antler much later, reaching a peak around late September (t_{max} = 8.7, Fig. 2c) when most adult males began to cast antlers (August-October). Juveniles cast antlers mostly during November-January as was evident from the fall in the hard antler curves for the two age classes (see Fig. 2, and Antler development). Yearling males (spikers) were out of phase with both adult and juvenile males. Thus, the percentage of yearling males in hard antler peaked around December (January in 1991 and December in 1992, t_{max} = 11.3, Fig. 2b). Thus adult and juvenile male peaks were separated by about 2.4 months, while juvenile and yearling male peaks were separated by 2.7 months. This was confirmed by time-lag correlation analyses. Comparisons were made between the antler cycles (monthly percentage in hard antler) of juveniles and adults and between juveniles and yearlings. In each case, they were each out of phase by about 2-3 months as shown by the higher and significant positive correlations at the corresponding lag (Fig. 3). Thus, yearling and adult males were out of phase by about 5.1 months.

These distinctly age-specific seasonal patterns were evident in 1991 and 1992, and even in the data for the first five months of 1993. Only

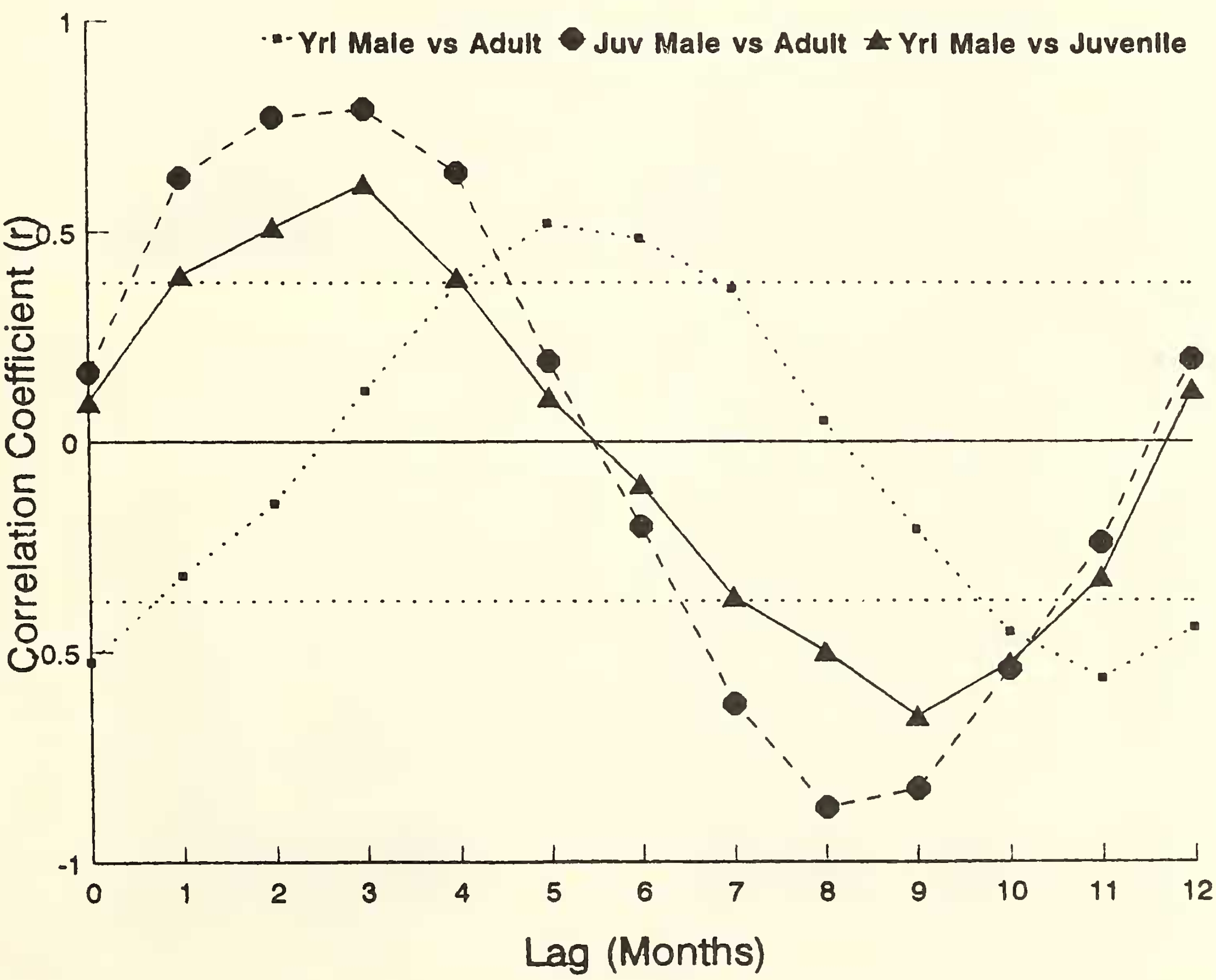

Fig. 3: Time-lag correlations between different age classes of male chital in the monthly percentage in hard antler. Pearson product-moment correlation values falling outside the range encompassed by the horizontal dotted lines are significant (2-tailed P < 0.05).

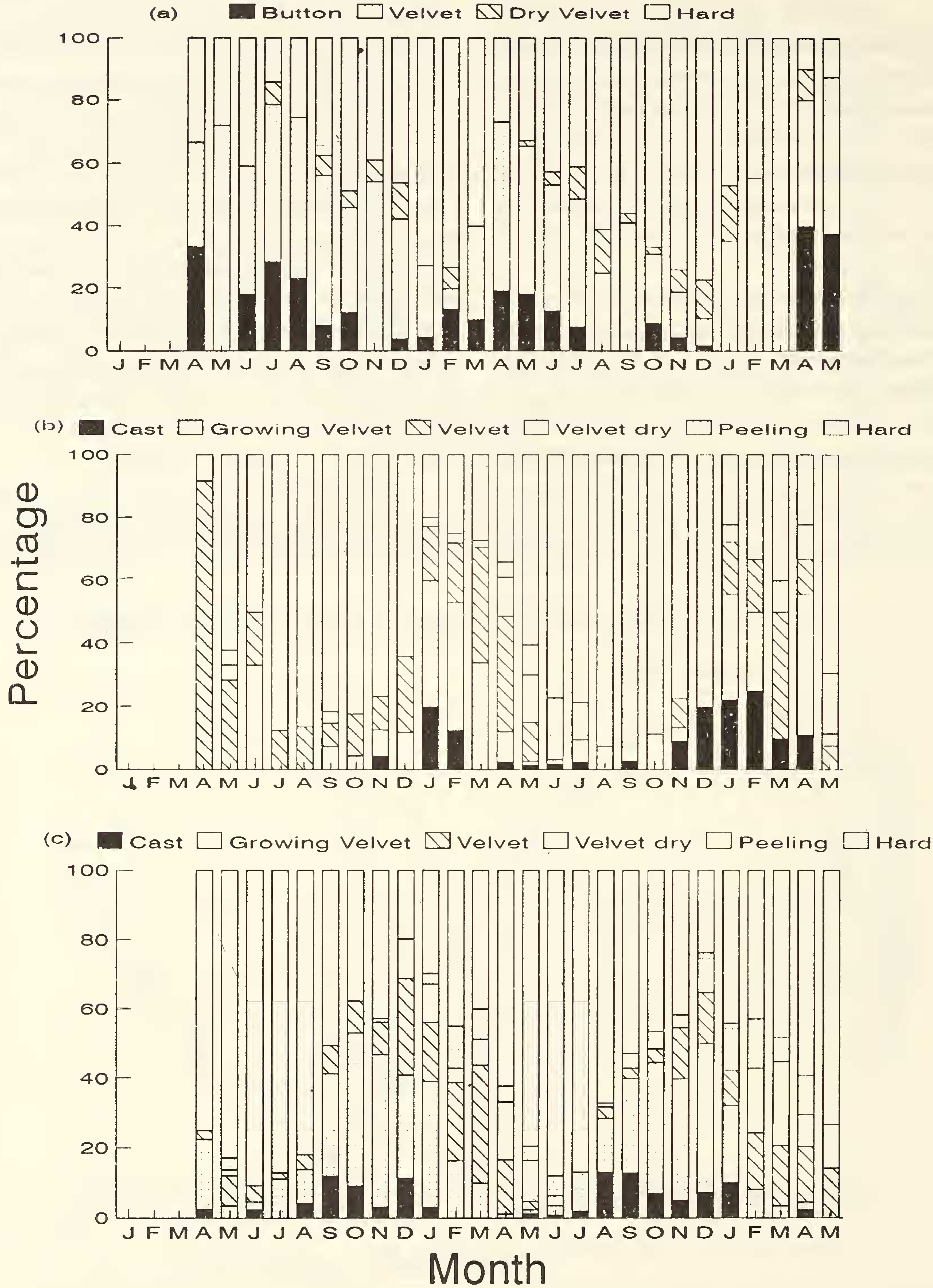

Fig. 4: Antler development in (a) Yearling Males, (b) Juvenile Males, and (c) Adult Males during 1991-93 as monthly percentage of individuals in different stages of antler development.

if males of all age classes are pooled, is an overall flatter curve obtained, indicating milder seasonality. It is clear, however, that even the pulse of age-specific seasonality is not absolute, as about 20% of the adult males were in hard antler even during the lowest month (December, but see Discussion).

Antler development according to age class

Consideration of different stages of antler development reinforces the above patterns. Yearling males in the 'Button Male' stage were observed as early as November-December, when they were 10-12 months old (assuming that they were born during the birth peak in January-February). A few button males were seen till about May-June the following year (Fig. 4a). During the following months, yearling males were mostly in velvet and dry velvet till about August-October, when many of them started turning from dry velvet into hard spikers over the winter. Most yearlings cast their antlers the following January-February, and the approximately 2-year old males now entered the juvenile age class.

The juvenile males were in growing and mature velvet till April-May; they cleaned their antlers of velvet, achieving their peak in hard antler between June and September (Fig. 4b). Interestingly, these were the months when most adult males had just cast their antlers (Fig. 4c). A majority of juveniles cast their hard antlers after December and entered the adult male age category as 3-year olds. These individuals then came into hard antler earlier than in the previous year, more or less in phase with the other adult males in the population. Between September and December, most adult males had growing antlers. By the following April, 60-75% of the adults had passed through the dry velvet and peeling phases to attain hard antlers and begin to rut.

Fawning seasonality

Births of fawns also clearly indicated seasonality (Fig. 5). The proportion of small fawns per 100 females peaked in February in 1992 and 1993. In 1991, a peak in births is also apparent in April, the reason for which is unknown. During 1991-92, most small fawns (49.2%) were noticed between December and March. Fawns two weeks to one month old could be seen moving with females. Based on the sizes of fawns in the field, my observations indicated that most births in GNP occurred between mid-December and mid-February. Very few births occurred between July and November. Only adult males showed a significant correlation between rutting (monthly percentage in hard antler) and fawning after a lag of 8-9 months, corresponding to the gestation period (Fig. 6).

Discussion

The antler cycle of chital in Guindy National Park appears, at first glance, to indicate a very diffuse seasonality as at least 50% of the males are in hard antler for 8 out of 12 months of the year. This has prompted observers in the past to conclude that chital breed aseasonally, even though each male may have its own yearly seasonal cycle (Inverarity 1895, Krishnan 1972, Lincoln 1992a,b, Loudon and Curlewis 1988). The present study shows, however, that the antler cycle of individual age classes of males reveals distinct seasonal patterns. Most of the adult males (73-91%) are in hard antler between March and July, with a peak in May-June. In contrast, juvenile and yearling males peak about 2.5 and 5 months later.

Such staggered antler cycles of different age classes of deer have been reported even in temperate cervids exhibiting greater seasonality of breeding such as the Sika deer *Cervus nippon* (Miura 1984a) and reindeer (Leader-Williams 1988). In red deer *Cervus elaphus*, dominant males tend to cast antlers (and come into hard

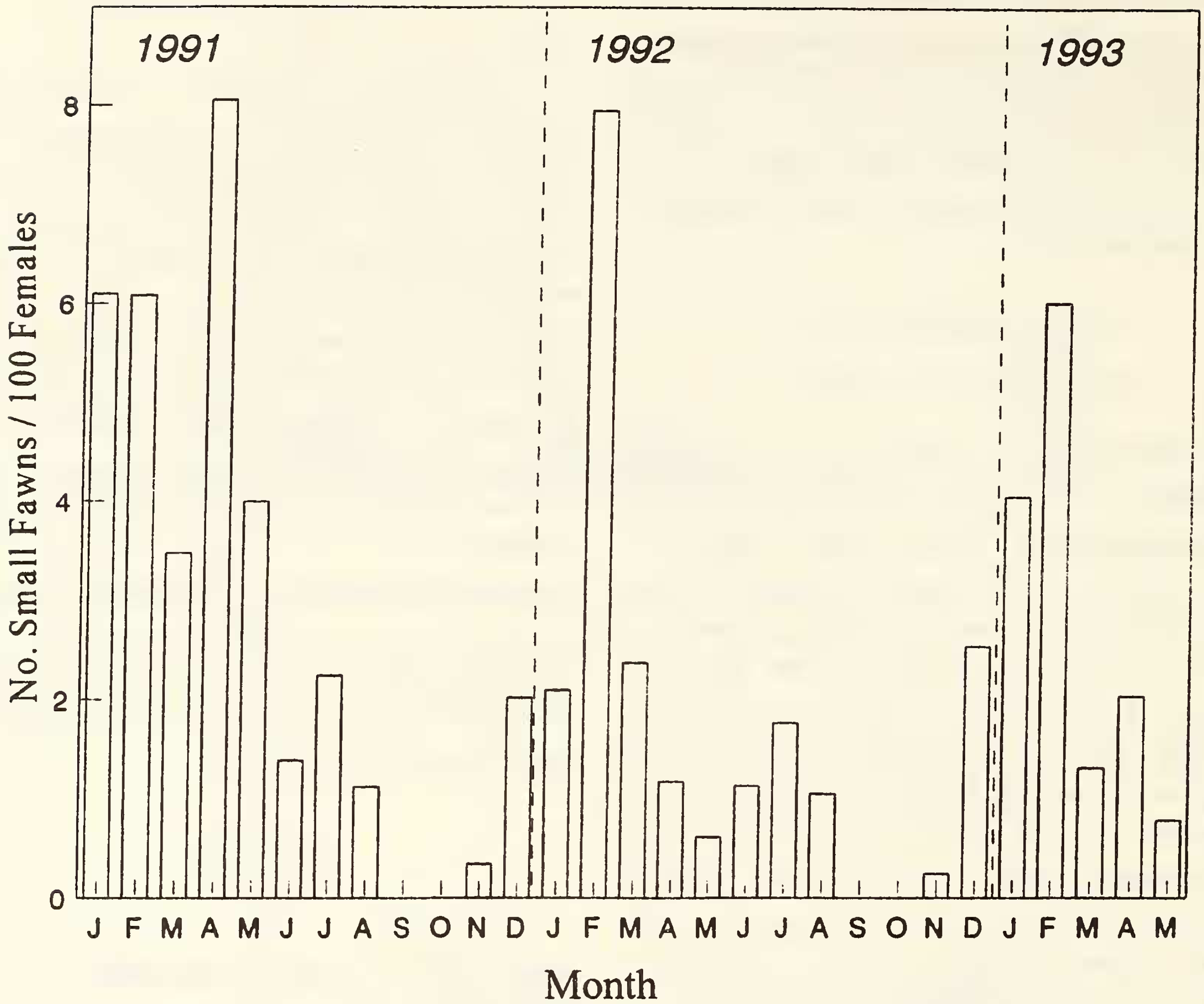

Fig. 5: Seasonality of fawning in chital in Guindy National Park from 1991-93.

antler) earlier and produce larger antlers than subordinate ones (Bartoš 1990). Yearling male chital have also been reported to come into hard antler several months after the peak in the adult rut (Fuchs 1977, Schaller 1967, Schaller and De 1971). Age-related differences in antler cycles and rutting have been noted in other Indian deer species: the swamp deer or barasingha (*Cervus duvauceli duvauceli* — young stags cast antlers later in the year, Singh 1984, and my personal observation), the hardground barasingha (*C. d. branderi* — young stags rut later than adults, Martin 1975), and the sambar (*C. unicolor* — young males cast antlers later than adults, Richardson 1972). In spite of the occasional description of these patterns, the processes underlying them remain poorly understood. Here I discuss the factors influencing the breeding seasonality patterns in male and female chital, and compare these with other cervids.

Age-related antler cycles and reproduction in males

It is well established that the hard antler stage in tropical and temperate cervids is associated with high testosterone levels, enlarged testes, and heightened sexual activity in males (Goss 1983, Lincoln 1985, 1992b, *Axis axis*: Loudon and Curlewis 1988). The rut is an energetically expensive period for males of different species due to the demands of territorial defence, mate searching, bellowing, sparring and fighting activities (Clutton-Brock *et al.* 1979,

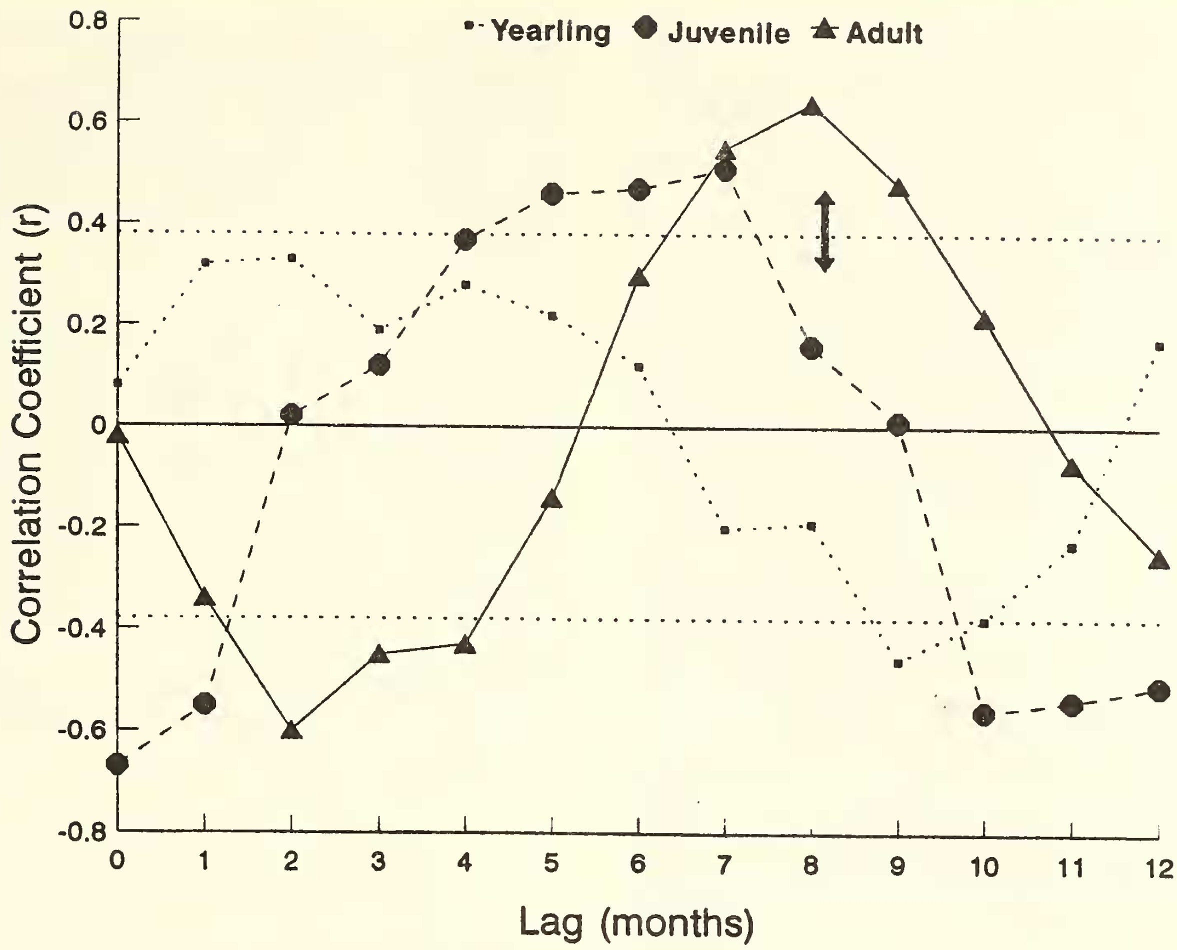

Fig. 6: Time-lag correlations between the monthly percentage of hard antlered males of different age classes and fawning. Pearson product-moment correlation values falling outside the range encompassed by the horizontal dotted lines are significant (2-tailed $P < 0.05$)

1982, Barrette 1987, de Vos *et al.* 1967, Schaller 1967) resulting in weight loss (Mitchell *et al.* 1976, Loudon and Curlewis 1988), stress (Bronson 1989), and injuries including mortal wounds (Clutton-Brock 1982, Clutton-Brock *et al.* 1979, 1982, Miura 1984b). In chital, bodily injury to males in vicious fights was observed in 18 of 74 instances in Texas (Fuchs 1977) and a high frequency of antler breakage was also noted (Barrette 1985, Fuchs 1977). Also, older hard-antlered male chital are more susceptible to predation than younger males (Johnsingh 1983, Patel 1992).

These observations are important when considering age-related differences in antler cycles. In GNP, by the end of May, nearly 70-80% of the adult males have been rutting for two months, and a further 5-10% have been rutting for a month. Thus in June, when most juvenile males attain hard antler, a majority of adult males are relatively exhausted from their rutting activities. If any females are in oestrus at this time or later, the chances for juvenile males to succeed in courtship may be higher. In fact, chital females are known to have a series of oestrus cycles throughout the year in captivity (Asdell 1964). Females that fail to conceive during the main rut of adult males, cycle again at intervals of about 19 days (English 1992), and may mate with juvenile or yearling males later in the year, when most adults are in velvet. Similarly, in red deer and reindeer, sub-adult stags achieve little success in obtaining and copulating with oestrus hinds during the mating peak of adult stags (Gibson and Guinness 1980, Hirotani 1994), but young stags that hold hinds later, when most adults are exhausted, achieve copulation (Clutton-Brock *et al.* 1982, Hirotani 1994). This is also analogous to *musth* in African elephants *Loxodonta africana*, where younger males often stagger their *musth* from large bulls, and are then able to dominate them in fights over oestrus females or access to resources (Poole 1989).

Thus, the staggered age-specific patterns of antler cycles can be a strategy to avoid intrasexual conflict among males. This may apply particularly in areas which have a high density of chital such as GNP (212.3 individuals/km^2, Raman *et al.* 1996). Another explanation given for such age-specific patterns of rutting is that the timing of antler development may be determined ontogenetically, so as to enable individual males to come into hard antler at the time of the main rut, when they attain adulthood (Dunbar-Brander 1931, Schaller 1967). This, however, does not appear to hold true, since in the lower-density (18.9 chital/km^2) free-ranging population of chital in Texas, Fuchs (1977) found that only yearling males differed in antler cycles from other males, whereas juvenile males were more or less synchronous with adult males. It is speculated that there may be flexible variation in antler cycles of males in different populations depending on the intensity of male-male conflict.

Younger males may stagger their antler cycles only if they are able to derive the benefits of conflict avoidance and attaining copulation. It was not within the scope of the present study to examine copulatory success of males of different age classes. Earlier studies have, however, shown that juvenile male chital do achieve copulation under free-ranging conditions (Barrette 1987). About 90% (61 of 68) of the copulations documented in the literature were achieved by the big male class (antler length > 60 cm), 6% (4) by medium males (antler length 30-60 cm), 4% (3) by juvenile males (antler length < 30 cm), and none by yearling males (Barrette 1987). From the female's point of view, mating with a younger male may be better than not mating at all in a given year. Conversely, younger males too could be of high quality and females could mate with young males which possess attributes that are relatively high-quality for their age (Clutton-Brock *et al.* 1982). Further studies are, however, required to produce direct behavioural evidence that can support or reject the contention that staggering of antler cycles by younger males in chital is a strategy to offset male-male conflict and attain higher reproductive success.

An offshoot of the age-specific patterns of rutting may be the slightly diffuse nature of the fawn birth pulse. Another reason for this is probably that seasonality in the tropics is less sharp than in temperate regions. Male fawns born outside the birth peak may contribute to the small proportion of 'floating' males which have their antler cycles out of phase with other males of their age class. The time of the year when males of different age classes rut is probably constrained by female breeding seasonality.

Female breeding seasonality

Given a gestation period of about 8 months in chital (English 1992: 235 days, SD = 3.0, Rao 1984: 236-247 days, $N = 5$), the results indicate that most conceptions occurred in May-June, corresponding to the peak in rutting of adult males (Fig. 2d). That adult males are responsible for most of the conceptions is supported by the significant correlation between the adult male rut and fawning at a lag of 8-9 months. Weaning of fawns occurs 3-4.5 months after birth (Graf and Nichols 1966) and the mean time between birth and the next conception has been estimated to be 48 days in captivity (English 1992) and 4-5 months in the wild (Graf and Nichols 1966). Females with big fawns close to weaning age are frequently observed being courted by chital males (Barrette *pers. comm.* and my own observation). Thus in GNP, weaning of most fawns and conceptions occur around May-June during the adult male rutting peak.

Female deer usually undergo parturition during periods that are most favourable for fawn survival, usually in terms of high food availability (Delany and Happold 1979, Robbins *et al.* 1987; Sempéré 1990). In GNP, however, most births occur between late December and early March, which is the onset of the dry season, a period of relative resource scarcity (Fig. 1). Observing similar seasonality in Bandipur, Sharatchandra and Gadgil (1975) suggested that females pursue this strategy as it entails pregnancy during the wet season, when food is abundant. In female deer and other ruminants, however, the energy needs of lactation are known to exceed those of pregnancy (Bronson 1989, Loudon and Brinklow 1992, Loudon and Kay 1984, Robbins *et al.* 1987, Widdowson 1981). The late-lactation period is, therefore, likely to be crucial both for maternal survival and investment in offspring. While quantitative data are lacking on chital feeding ecology and nutritional energetics, it is suggested that, in places such as GNP and Bandipur, parturition by females at the onset of the dry season enables them to coincide their period of late-lactation with the flush of plant growth following pre-monsoon showers. After weaning, the fawns begin to feed on the grasses from the southwest monsoon rains. Pregnant females can then meet the needs of foetal development through the wet season, and store reserves for the needs of the dry season, birth, and early lactation (Sharatchandra and Gadgil 1975).

The influence of rainfall and food availability can be tested on different chital populations. It can be predicted that in north India, where the monsoon occurs about a month later, breeding would be delayed. Available reports as well as this study partially support this conjecture. Thus chital in Bandipur and GNP at 13°N have a rutting peak in May-June (Johnsingh 1983, Sharatchandra and Gadgil 1975), while in Corbett National Park at 29°N it is in June-July (Tak and Lamba 1984). In Chitwan National Park at the same latitude, however, the peak rut is in April-May (Mishra and Wemmer 1987), which may be due to early pre-monsoon rains in April-May or due to factors other than rainfall. Interestingly, in Wilpattu National Park in Sri Lanka where there are two distinct rainy seasons, there are two corresponding fawning seasons in the chital population (Eisenberg and Lockhart 1972, Barrette *pers. comm.*). Quantitative description of such patterns in future studies using sinusoidal curves as presented in this study will enable comparison of biologically relevant parameters across populations. Studies of captive herds coupled with long-term field studies can yield comprehensive insights into the factors affecting the reproduction of tropical cervids.

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